AMERICAN MUSEUM NOVITATES

Published by
Number 1301 THE AMERICAN MUSEUM OF NATURAL HISTORY November 6, 1945
New York City

THE HYOID BONES IN *PROTOCERATOPS* AND IN *PSITTACOSAURUS*[1]

BY EDWIN H. COLBERT

INTRODUCTION

During the preparation of a skeleton of *Protoceratops*, Mr. Otto Falkenbach of the American Museum Paleontological Laboratory discovered two small bones which when first seen appeared to be quite unlike any elements hitherto known in this dinosaur. At first it was thought that these bones might be portions of the sternum, but comparisons soon showed that such could not be the case. Indeed, various comparisons with the known osteological elements of *Protoceratops* confirmed the first impression, namely, that these were bones hitherto undescribed, so the question arose as to what these bones might be. Several possibilities were considered and several opinions were sought, with the result that Dr. William King Gregory of the American Museum suggested that these might be hyoid elements. The more this possibility was investigated, the more likely it seemed to be. All subsequent investigations have tended to confirm this view.

It has been felt desirable to bring out a description of these supposed hyoid bones, in order that the published knowledge concerning *Protoceratops*, contained in several papers but especially in the study by Brown and Schlaikjer (1940), may be as complete as possible. At the same time, it was felt that certain comparisons with other dinosaurs of varying relationships to *Protoceratops* should be included in this study. Such is the subject matter that will be treated in the following pages.

The author wishes to express his appreciation to Mr. Falkenbach, who in the course of his skillful preparation of the specimen of *Protoceratops* made the discovery of these new bones. To Dr. Gregory must go the credit of making the suggestion as to their being hyoids, and to him my fullest acknowledgments are hereby expressed. Subsequently a portion of another bone was found, and this may represent an additional element in the hyoid apparatus of *Protoceratops*. The translation from Fürbringer was made by Dr. Otto Haas. Finally credit should go to Mr. John C. Germann, Staff Artist, for the excellent illustrations that appear in this paper.

DESCRIPTION AND DISCUSSION

Before making a formal description of these supposed hyoids of *Protoceratops*, it may be well to consider briefly the homologies of the hyoid bones in the tetrapods, and their development particularly in modern reptiles.

A very illuminating statement describing the development and the homologies of the hyoids in modern reptiles was set forth by Fürbringer in his monograph on the hyoids of the vertebrates (1922). A translation of this statement follows:

"As has been known in the main for a long time, the hyoid of living reptiles consists, at its highest stage of development, of an unpaired body, the corpus (Copula; basihyal and basibranchial) [basibranchial and hypobranchial according to Goodrich]

[1] Publications of the Asiatic Expeditions of the American Museum of Natural History, Contribution No. 148.

tapering in a forward direction into a narrower process, the *processus lingualis* (processus entoglossus), which varies in length and is bound into the posterior part of the tongue, and of three pairs of horns connected laterally in various ways with the corpus, an anterior pair, the cornu hyale, a middle pair, the cornu branchiale I, and a posterior pair, the cornu branchiale II, and these are derived from the ordinary hyoid arch and the first two gill arches. In the more primitive forms the cornu hyale is found to be connected with the columellar apparatus of the middle ear, also, an element in the hyoid arch, but this connection has been lost in most of the reptiles and has undergone considerable reduction in many of them. This horn is very significant morphologically and therefore has been named the cornu principale by Gaupp, but it is inferior in size and strength to the following horn. This horn, the *cornu branchiale* I, which is derived from the first branchial or third visceral arch, is dorsally free and it proves by its permanence and by the fact that it is ossified when all other

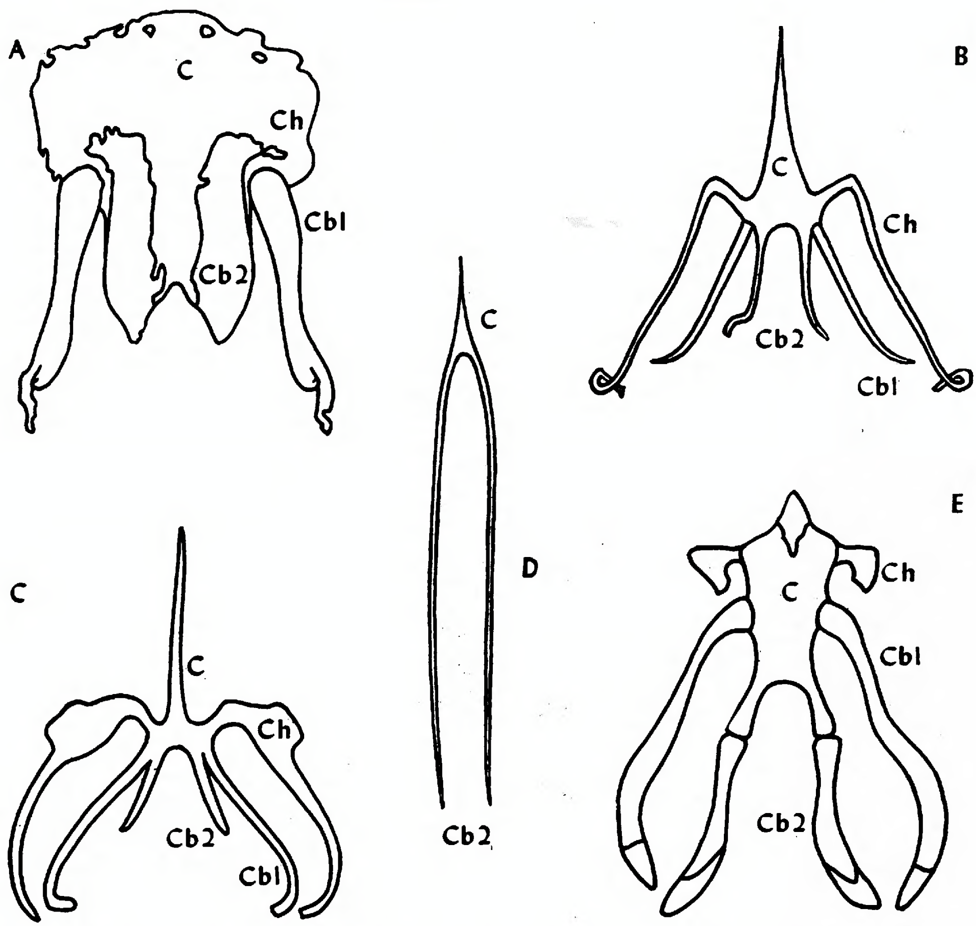

Fig. 1. A comparison of the hyoids in the living reptiles. A, Crocodilia: *Crocodilus*, original. B, Rhynchocephalia: *Sphenodon*, after Fürbringer. C, Squamata: *Lacerta*, after Goodrich. D, Squamata, *Vipera*, after Fürbringer. E, Chelonia: *Clemmys*, after Fürbringer. Not to scale. Key to abbreviations: C—corpus, including the hypohyal or entoglossal. Ch—ceratohyal and epihyal; cornu hyale. Cb1—ceratobranchial I; cornu branchiale I. Cb2—ceratobranchial II; cornu branchiale II.

portions of the hyoid are cartilaginous, to be the most prominent part of the hyoid complex. The *cornu branchiale* II, derived from the second branchial or fourth visceral arch, is considerably reduced, and frequently in many reptiles it is split up into a ventral and a dorsal portion, while it may disappear completely in some forms. This horn, too, is as a rule dorsally free, but in some isolated cases it is connected with the dorsal end of the cornu hyale. Starting with the highest level of development, the hyoid of many reptiles, most of which may be considered as advanced forms, is subject to reduction. This may start sometimes with the first horn, the cornu hyale, sometimes with the last one, the cornu branchiale II, or it may take place simultaneously at the anterior and posterior ends.

"(For a more detailed survey, reference is made to Gaupp's excellent synthesis of the ontogeny and phylogeny of the sound conducting apparatus in vertebrates as well as of the evolution of the cranial and the hyobranchial skeleton.)

"Simultaneously the hyoid bone constitutes in various ways the ventral basis and, when well developed, the support for the respiratory organs (larynx, i.e., cricoid, with adjacent cartilages, the trachea). The connection between both is sometimes loose, sometimes solid, and it may exist between hyoid and cricoid or between hyoid and trachea, with all transitions from the cricoid to the trachea" (Fürbringer, 1922, p. 6).

For the purpose of orienting ourselves and avoiding a long, detailed discussion, the manner in which the hyoid apparatus is developed in the modern reptiles may be shown by a diagram in which typical examples of the hyoids in turtles, rhynchocephalians, crocodilians, lizards, and snakes are pictured. This diagram will, of course, supplement the summary written by Fürbringer and presented above. Homologies are derived from a comparison with the condition in fishes.

Various names have been applied to the hyoid elements shown in this diagram. It may be well, therefore, to include at this place a table to show the system of nomenclature used for the hyoid elements by Fürbringer in 1922, as compared with the system used by Goodrich in 1930, and that followed by Camp in his classification of the lizards, 1923, and more recent papers.

Fürbringer	Goodrich	Camp
Corpus	Corpus or Copula	Corpus
Entoglossal	Entoglossal process	Hypohyal
Cornu hyale	Hyoid cornu	Ceratohyal Epihyal
Cornu branchiale I	First branchial cornu	Ceratobranchial I Epibranchial I
Cornu branchiale II	Second branchial cornu	Ceratobranchial II Epibranchial II

In the present work Camp's terminology is used.

In this present discussion our interest, as far as recent reptiles are concerned, is centered upon the Crocodilia since these animals, most closely among the living forms, approach the dinosaurs in their morphological development.

The hyoids of the Crocodilia are described at some length by Fürbringer, who shows that in these reptiles the hyoids consist of a large corpus, ventrally convex, from the side of which project large, well-ossified first ceratobranchials. The corpus is cartilaginous and broader anteriorly than posteriorly. In its dorsal concavity are the cricoid and arytenoid cartilages.

According to Fürbringer, the existence of a ceratohyal is not certain in the Crocodilia. It would seem probable, from the ontogenetic work of Parker, that it was suppressed at an early stage of development.

The first ceratobranchial, says Fürbringer, projects from the lateral border of the corpus and is directed somewhat laterally and somewhat dorsally. This is a very strong, highly ossified element, which often shows, according to the age of the

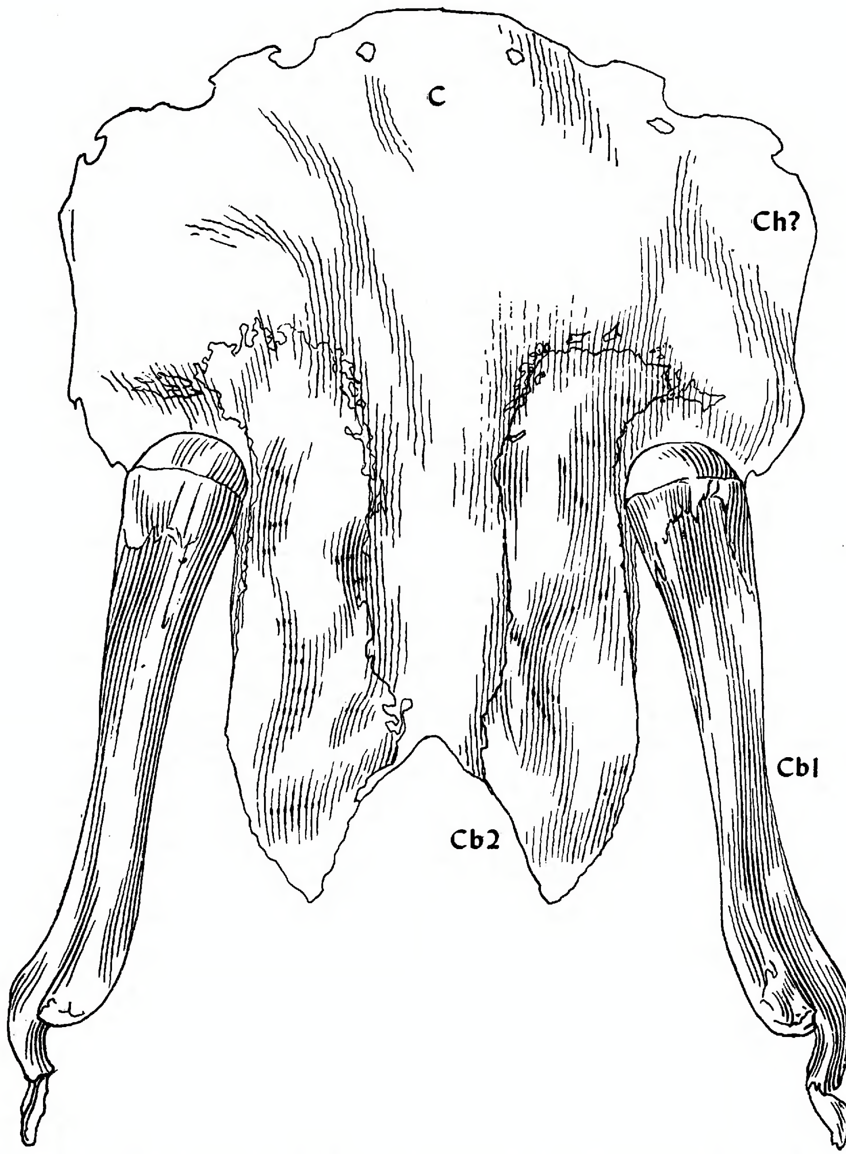

Fig. 2. The hyoid apparatus of *Crocodilus porosus*. Ventral view, natural size. Abbreviations as in figure 1.

animal or the species, a longer or shorter cartilaginous epiphysis at the free end. In young embryos this element is cartilaginous, but it begins to ossify during embryonic life.

The second ceratobranchials are contained in the two posterior corners of the hyoid body or corpus. It might be helpful at this place to supplement briefly Fürbringer's remarks as to the hyoids in the Crocodilia, condensed and paraphrased above, with a few notes regarding the hyoids of *Crocodilus porosus* as shown by a specimen at hand. Evidently this came from a fairly large animal, so that ossification has proceeded to a considerable extent.

The corpus or copula, however, is completely cartilaginous. It is broad, and its lateral edges are extended; these may represent in part at least the ceratohyals,

As Fürbringer has shown, this is a debatable question upon the basis of such evidence as is now available to us.

The corpus extends imperceptibly into the second ceratobranchials, which are bony. However, the line of separation between each bony cornu and the cartilaginous body of the copula is not definite, and the two merge into each other. Along the edges the bony cornua are invested by cartilage. The first ceratobranchials protrude from the corpus near the anterior ends of the second ceratobranchials. These first ceratobranchials are completely bony and L-shaped, and their anterior ends, articulating with the corpus, are rounded into "heads." At the angle of the "L" a distinct point is produced. Posteriorly these bones show cartilaginous connections. This specimen is illustrated in figure 2.

With this orientation of the subject in mind, we may now consider the fossil materials that are the basis for this study. Of first importance are the two paired bones that were associated with the *Protoceratops* skeleton, A.M.N.H. No. 6471.

These bones are shown in figure 3, and reference to this illustration will give an idea as to their form to much better advantage than may be had from any word description. These bones are thin and essentially flat, although at their expanded ends they are on one side slightly concave and on the other slightly convex. Each bone is expanded laterally at either end and constricted in the middle, and one side is in the form of a simple, flattened curve, with a somewhat thickened edge. The other edges of the bone are all very thin except at the ends near the juncture of the rounded end surfaces with the simply curved side. Here the edges are thickened.

It is supposed by analogy with the Crocodilia that these flattened bones in *Protoceratops* are the second ceratobranchials. Assuming this to be so, how are these elements to be oriented? This is a difficult question, because unfortunately these bones are shaped somewhat differently from the second ceratobranchials in the Crocodilia.

It would seem most probable, however, that the long, simply curved, and somewhat thickened edge of each bone is the lateral one, and the thin, sinuous curved edge the median one. This would accord with the condition in the Crocodilia, in which the median edges of the second ceratobranchials thin out so that they merge gradually with the cartilage of the corpus. Further support for this orientation of the bones is

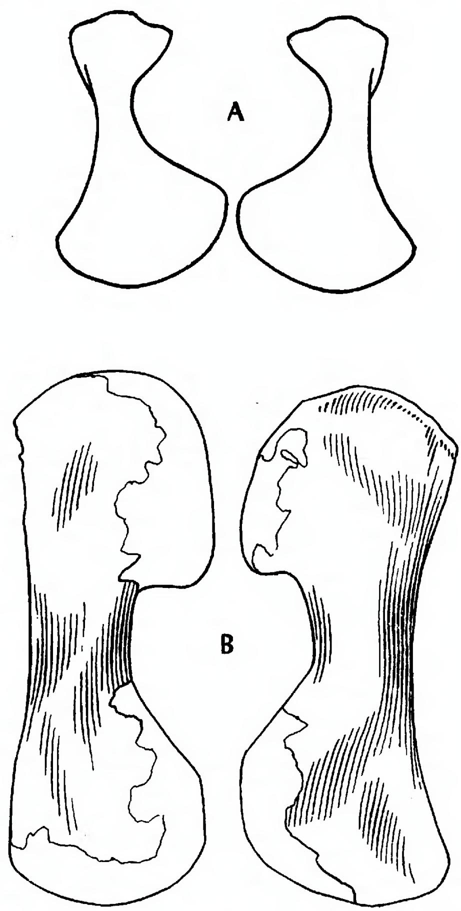

Fig. 3. A, The hyoid bones (probably the second ceratobranchials) of *Limnoscelis*, as preserved in position. After Williston, not to scale. B, The supposed second ceratobranchials of *Protoceratops*. A.M.N.H. No. 6471. Ventral view, natural size. In both drawings the bones are oriented with their assumed anterior ends up.

afforded by the hyoids of *Limnoscelis*, figured by Williston in 1911. Williston found that in *Limnoscelis*, a very primitive Permian cotylosaur, there was a pair of bones which he interpreted as hyoids, and which he described as follows:

"In each skeleton there is a pair of bones .... of the nature of which I am not fully satisfied, though there would seem to be little doubt but that they are unusually large hyoids. They are .... greatly expanded on their distal, thin end, with a somewhat curved and narrowed shaft deeply concave in outline on one side, less so on the other, thickened and truncate for articulation at the proximal end. The two bones in each specimen lie with the thin ends nearly in apposition, as though they had joined each other in life" (Williston, 1911, pp. 36–37).

These bones, which are shown in outline in figure 3, bear a considerable resemblance to the supposed hyoids of *Protoceratops*, as may be seen. Since the hyoids in *Limnoscelis* are in position, with the thin, sinuous edges opposite each other, it is logical to assume that the hyoids in *Protoceratops* were oriented in a similar manner.

As to the question of the anterior and posterior ends of the supposed hyoids in *Protoceratops*, this is a difficult problem to solve. The bones have been oriented as shown in figure 3, with the full realization that further information at some future date may require their reversal, end for end. At any rate, the orientation of the bones as shown seems to correspond most closely with the orientation of the hyoids in *Limnoscelis*, and for the time being this will have to serve as the guide to their position.

Finally, it may be rather safely assumed that the convex surface of each bone in *Protoceratops* is the ventral surface, and that the concave surface faced dorsad, as is the case in the crocodiles.

In addition to these two flat bones, still another small bony fragment of puzzling relationships was found in association with the same *Protoceratops*, namely, A.M.N.H. No. 6471. This is a thin, forked bone, of which it would seem that most of the length of the two forks has been lost. This bone has a sort of small hook or process opposite one of the forks. Here again, a figure gives a much more adequate idea as to the structure of the element than does a word description.

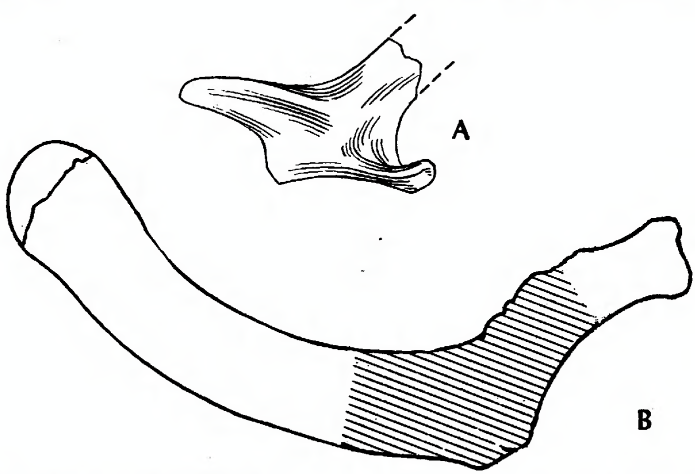

Fig. 4. A, Portion of a bone found in association with *Protoceratops*, A.M.N.H. No. 6471, and identified as possibly a part of the first ceratobranchial. B, Outline of the first ceratobranchial of *Crocodilus porosus*. That portion of the bone supposed to be homologous with the *Protoceratops* bone above (A) is shaded. External lateral views, both natural size.

Frequent attempts to homologize this bone as a portion of a rib have proved to be quite unsatisfactory. Nor is there any other element known in the skeleton of *Protoceratops* with which this bone is closely comparable. Therefore it is suggested that this may be a portion of a first ceratobranchial. In *Crocodilus porosus* the first ceratobranchial, as already mentioned, is an L-shaped bone, with a point developed at the angle of the L. Perhaps this fossil fragment comes from the same general re-

gion of the angle in the first ceratobranchial of *Protoceratops* with a possible position as shown in the figure. This may be an erroneous interpretation, but no other satisfactory explanation suggests itself at the present time.

In making this study of the hyoids in *Protoceratops*, a reëxamination of the dinosaur *Psittacosaurus* was made. *Psittacosaurus*, described by Osborn in 1924, comes from the Ondai Sair formation of Mongolia, which makes this form somewhat older than *Protoceratops*. Moreover, there is every reason to think that *Psittacosaurus* is very close to, if not actually on, the ancestral line leading to the Ceratopsia, a point that was made by Gregory in 1927, but that has never received the attention it deserves. Indeed, it is proposed at this place to include *Psittacosaurus* in the suborder Ceratopsia, rather than in the Ornithopoda where it was placed by Osborn, who has been generally followed by subsequent authors.

Despite Osborn's excellent preliminary paper on this genus, *Psittacosaurus* has never been fully described. Consequently many various interesting features characterizing this important little dinosaur are still to be recorded in the literature. In the type skull, A.M.N.H. No. 6254, there is a mass of matrix and bones occupying the space between the rami of the mandible, and because of the information that might be obtained with regard to this question of the hyoids in dinosaurs it was thought expedient to develop this region in the type specimen. The task was undertaken and accomplished by Mr. Falkenbach with his usual skill.

As a result of Mr. Falkenbach's further preparation of the specimen, certain bones came to light that seem without much doubt to be hyoids. These occupy the position in which hyoids might be expected, and they can be eliminated from consideration as cervical ribs because of their shape and size.

They consist of two flattened bones, side by side between the mandibular rami, and two long, rod-like bones. Of the latter, one lies between the two flat bones and in the same plane with them; the other, at right angles to this plane, extends from near the posterior border of the right flat bone to a point beneath the basioccipital of the skull. This latter bone is closely appressed to the cervical vertebrae.

By analogy with the Crocodilia the flat bones are here identified as the flattened second ceratobranchials, while the elongated bones are considered as the first ceratobranchials.

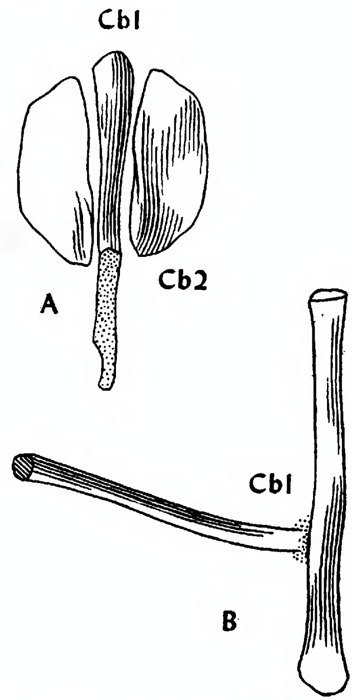

Fig. 5. Hyoid bones in *Psittacosaurus*. A, A.M.N.H. No. 6254. B, A.M.N.H. No. 6534. Ventral views, both figures natural size. Key to abbreviations: Cb1—ceratobranchial I. Cb2—ceratobranchial II.

Strictly speaking, the supposed second ceratobranchials are neither exactly "flat" nor truly bony. Careful examination under the microscope indicates, by reason of the manner in which they are preserved, that these elements were never fully ossified in life but rather were cartilaginous. Therefore these elements may represent the second ceratobranchials and to some extent portions of the corpus, but here a definite conclusion is not possible. They are somewhat convex ventrally, as might be expected, and in each the postero-in-

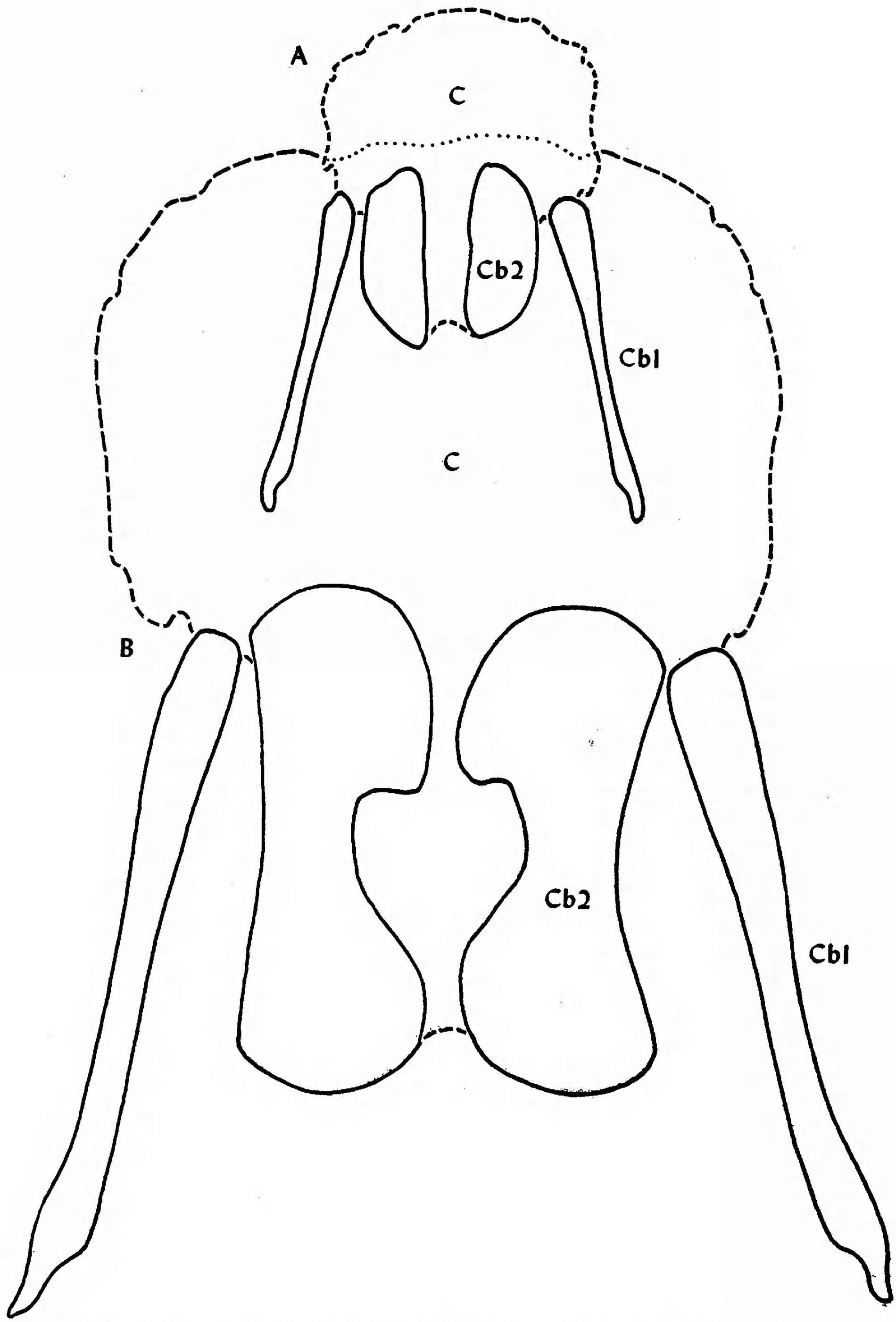

Fig. 6. Restoration of the hyoid apparatus in (A) *Psittacosaurus* and (B) *Protoceratops*. Ventral views, natural size. Key to abbreviations: C—corpus. Cb1—ceratobranchial I. Cb2—ceratobranchial II.

ternal corner is lower than the major portion of the element. It is an interesting fact that a small portion of this postero-internal corner shows a high degree of ossification in just the region where ossification of the second ceratobranchial might be expected. In shape each of these bones has a straight, internal, median edge and a curved, external, lateral edge, and the antero-internal and postero-internal corners are somewhat produced.

The supposed first ceratobranchials are elongated, rod-like bones and are fully ossified, as might be expected. These bones are comparatively straight, and their ends are rounded.

Another specimen of *Psittacosaurus*, A.M.N.H. No. 6534, also shows two loose bones in the basicranial region that are similar in shape to the long bones described above in A.M.N.H. No. 6254 and for this reason are identified as the first ceratobranchials of the hyoid complex. These bones, as exposed in the specimen, are shown in figure 5.

Jaeckel, in his paper of 1913 describing *Plateosaurus*, mentions and figures two large hyoid bones which were found beneath the lower jaws in one of the specimens under his observation. These are very long, rod-like bones, somewhat broadened at their posterior ends. They are obviously homologous with the first ceratobranchials as they are developed in the Crocodilia; indeed this conclusion seemingly was reached by Jaeckel, because he speaks of the "sogenannten Zungenbeinhorner," a term that has been applied to the first ceratobranchials by several German writers.

In this connection it might be pointed out that Gilmore, in 1925, described very briefly some hyoid bones associated with a skull and lower jaws of *Camarasaurus*, in the collections of the Carnegie Museum, Pittsburgh.

"That there is a well developed hyoid apparatus in the Sauropod dinosauria is shown by the preservation in the matrix beneath the lower jaws of three rod-like bones, which undoubtedly represent elements of the hyoid arch. The longest of these measures 165 millimeters in length. Two of them are paired and probably represent the thyrohyal bones" (Gilmore, 1925).

The two long paired bones mentioned by Gilmore are almost certainly the long, bony, first ceratobranchials, the homologues of the thyrohyals in the mammals. What the third bone may be is a debatable question. From Gilmore's figure (pl. 15) this appears to be a rod-like bone, considerably shorter than the paired bones. Perhaps it is a second ceratobranchial.

CONCLUSIONS

From the evidence at hand it would appear that the hyoid bones in the dinosaurs show a development rather similar to that in the modern Crocodilia. In other words, it is probable that in the Saurischia and the Ornithischia the hyoid apparatus took the form of a broad corpus, perhaps for the most part cartilaginous, in the posterior portion of which there were enclosed the paired, flattened, second ceratobranchials. These elements were ossified to a greater or lesser degree. From this broad, plate-like fusion of the corpus and cornua there protruded the long, rod-like, first ceratobranchials. These elements, which were highly ossified and are generally the bones preserved, were attached at one end near the antero-lateral borders of the second ceratobranchials and were directed posterolaterally into the region of the throat. If this picture of the hyoid development in the dinosaurs is correct it is in accord with other morphological characters which show the relationship between these two extinct orders and modern Crocodilia.

In figure 6 the hyoid apparatus is restored in *Psittacosaurus* and in *Protoceratops* on the basis of the known condition in *Crocodilus*.

REFERENCES

Brown, Barnum, and Erich M. Schlaikjer
1940. The structure and relationships of *Protoceratops*. Ann. New York Acad. Sci., vol. 40, art. 3, pp. 133–265, pls. 1–13.

Camp, Charles
1923. Classification of the lizards. Bull. Amer. Mus. Nat. Hist., vol. 48, pp. 289–481.

Fürbringer, Max
1919. Über das Zungenbein der Reptilien. Bijd. Dierk., no. 21, pp. 195–212.
1922. Das Zungenbein der Wirbeltiere insbesondere der Reptilien und Vögel. Abhandl. Heidelberg Akad. Wiss., div. B, vol. 11, 164 pp., 12 pls.

Gilmore, C. W.
1925. A nearly complete articulated skeleton of Camarasaurus, a saurischian dinosaur from the Dinosaur National Monument, Utah. Mem. Carnegie Mus., vol. 10, no. 3, pp. 347–384, pls. 13–17.

Goodrich, Edwin S.
1930. Studies on the structure and development of vertebrates. London, Macmillan and Co., pp. 440–448.

Granger, Walter, and William K. Gregory
1923. *Protoceratops andrewsi*, a pre-ceratopsian dinosaur from Mongolia. Amer. Mus. Novitates, no. 72, pp. 1–9.

Gregory, William K.
1927. The Mongolian life record. Sci. Monthly, vol. 24, pp. 169–181.

Gregory, William K., and Charles C. Mook
1925. On *Protoceratops*, a primitive ceratopsian dinosaur from the Lower Cretaceous of Mongolia. Amer. Mus. Novitates, no. 156, pp. 1–9.

Huene, F. von
1926. Vollständige Osteologie eines Plateosauriden aus dem schwäbischen Keuper. Geol. und Paleont. Abhandl., new ser., vol. 15, no. 2, pp. 139–179, pls. 7–13.

Jaekel, Otto
1913. Über die Wirbeltierfunde in der oberen Trias von Halberstadt. Palaeont. Zeitschr., vol. 1, no. 1, pp. 155–215, pls. 3–5.

Osborn, Henry Fairfield
1924. *Psittacosaurus* and *Protiguanodon:* two Lower Cretaceous iguanodonts from Mongolia. Amer. Mus. Novitates, no. 127, pp. 1–16.

Owen, Richard
1850. Communications between the cavity of the tympanum and the palate in the Crocodilia. Phil. Trans. Roy. Soc. London, pp. 521–527, pls. 40–42.
1859. On some reptilian fossils from South Africa. Proc. Geol. Soc. London, vol. 16, pt. 1, pp. 49–63, pls. 1–3.

Parker, W. K.
1883. On the structure and development of the skull in the Crocodilia. Trans. Zool. Soc. London, vol. 11, pt. 9, pp. 263–310, pls. 62–71.

Sushkin, P. P.
1927. On the modifications of the mandibular and hyoid arches, and their relations to the brain case in the early Tetrapoda. Palaeont. Zeitschr., vol. 8, pp. 263–321.

Williston, Samuel W.
1911. American Permian vertebrates. Chicago, University of Chicago Press, 145 pp., 38 pls.

Zavattari, Edoardo
1908. Materiali per lo studio dell' osso ioide dei Sauri. Atti. Accad. Sci. Torino, vol. 43, pp. 1138–1145.